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Editorial

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Introduction to the special column: communication, cooperation, and cognition in predators

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Communication is the glue that holds societies together and we might expect that highly social species with more to communicate about will have more complex communication systems and more complex cognitive abilities. Social species gain benefits from living in groups, and many of these benefits rely on intra-group communication. For example, predator-specific alarm calls can lead to different evasion responses (Suzuki 2014), or difficult to obtain food resources can be acquired using aggregation calls (King and Janik 2015).

Thinking about the logical relationships between social complexity and communicative complexity date back to Larmark and Darwin but only more recently has been formalized into the Social Complexity Hypothesis (SCH) that states "... groups with more complex social systems require more complex communicative systems to regulate interactions and relations among group members (Freeberg et al. 2012). Freeberg et al. (2012) special issue of the *Philosophical Transactions of the Royal Society B* provides a comprehensive, and timely evaluation of the SCH. It is logically related to the social or Machiavellian Intelligence Hypothesis, MIH (Byrne and Whiten 1989) and the Social Brain Hypothesis, SBH (Brothers 2002; Dunbar 2003) both of which emphasize the increased cognitive capabilities required for complex social living. Thus, communication, sociality, and cognition are logically intertwined with each other. And, as Freeberg and Krams (2015) point out, highly vocal species cooperate via calling behavior, so we can hypothesize that highly cooperative species may mediate their cooperation via vocalizations.

The existence of at least a correlative relationship between cooperation and cognition has been noted by multiple researchers, and forms the basis of the SBH (Brothers 2002; Dunbar 2003) and the MIH (Byrne and Whiten 1989). Recently, a link between social complexity and communicative complexity has also been observed (Freeberg and Krams 2015), indicating the existence of a tripartite behavioral complex, in which communication, cooperation, and cognition (CCC) appear to be positively correlated with each other. However, the causal relationships between these three behaviors remain unclear.

Proponents of the SBH suggest that increased cognition (and with it, increased neocortical volume) evolved as a mechanism to track complex inter-individual relationships in social groups (Dunbar 1993, 2003; Sewall 2015). Others suggest that ecological factors may have driven increased cognitive ability, enhancing the potential of animals to benefit from social aggregations (Barrett et al. 2007; Barrett and Würsig 2014).

The evolution of complex communication is even less clear, with some suggestions that communicative signals evolved as a result of living in large groups (McComb and Semple 2005), whereas evidence from birds suggest that existing communicative abilities could have been exapated to support coexistence in larger aggregations (Krams *et al.* 2012). However, complexity in sociality and communication has not received the attention it deserves outside sciurid rodents, birds, and primates (Sewall 2015).

Much of the debate on these topics centers on the few study systems that have been extensively investigated for support of the SBH/MIH, in particular, non-human primates. While some criticism may be justified that a focus on primate behavior may lead to anthropomorphism of ecological context (Barrett and Würsig 2014), a stronger argument in favor of widening the taxonomic base of CCC studies is that general evolutionary mechanisms are more likely to become apparent when examining a wider range of niches and adaptations. The generalizability of the SBH and MIH have been called into question (Barrett et al. 2007; Bergman and Beehner 2015), and additional taxa must be studied that meet the criteria of cooperative behavior and well-developed cognition. Model systems such as social carnivores appear to be a fruitful direction of study, and interestingly these species often also show highly sophisticated communication (Drea and Carter 2009). What were the evolutionary processes leading to this tripartite behavioral complex? And what can it tell us about the evolution of human CCC?

From an evolutionary perspective, it may be constructive to begin by thinking about what explains variation in acoustic structure and repertoire size. The SBH proposes that complex cognition is an adaptation to social living, and the SCH extends this to an explanation of complex communication (Freeberg and Krams 2015). However, the emphasis on non-human primates, and the emphasis on explaining brain size in terms of social complexity may neglect the importance of other social and ecological factors driving cognition, such as cooperative foraging in dolphins (Barrett and Würsig 2014), or limitations on physical brain size in otherwise highly social and cooperative species such as hyenas (Holekamp et al. 2013).

This also leaves open the question of how cognitive and communicative complexity arose in the first place. It is constructive to address the precise drivers of acoustic structure and repertoire size in non-primate species. For instance, group size drives the evolution of individualistic alarm calls in sciurid rodents (Pollard and Blumstein 2011, 2012) while social complexity drives the evolution of repertoire size (Blumstein and Armitage 1997; McComb and Semple 2005; Blumstein 2013).

The application of formal social network analyses across a wide range of species has permitted us to identify a suite of specific social attributes, but which attributes are relevant to models of cognition remains unclear (Bergman and Beehner 2015). In addition, there remains a challenge to identify how these attributes map onto specific acoustic features and communicative abilities. More generally, however, these social attributes may be uniquely associated with specific types of cooperative behavior. For instance, Flack et al. (2006) showed that third-party policing maintains cooperative interactions in pigtailed macaques *Macaca nemestrina* and permits more complex social interactions to emerge. Without policing, macaque aggression fragments the social group into smaller and less stable social niches.

Meaning, arguably the most complex aspect of communication emerges both directly from signal structure when noisy, nonlinear vocalizations elicit enhanced responses (e.g., Slaughter et al. 2013; Blesdoe and Blumstein 2014), and from increased cognitive abilities (e.g., cooperative foraging in dolphins King and Janik 2015). These cognitive abilities may then influence the nature of cooperation, or cognitive abilities that evolved for social interactions may be exapted to permit more information and hence meaning from contextually variable vocalizations.

Although these proposed evolutionary pathways to communicative complexity are appealing, to understand them more precisely we need to identify model systems with sufficient complexity to allow us to identify common themes and variations.

We are not the first to propose that social carnivores are such a system to investigate the links between CCC (Drea and Carter 2009). Social carnivores engage in a number of complex cooperative social behaviors (Smith et al. 2012; Bailey et al. 2013). Some species coordinate movement through space, while others maintain social cohesion. Some cooperatively hunt and by doing so are able to take down larger prey than they could alone (Escobedo et al. 2015), while others cooperatively defend their food from both conspecifics and heterospecifics (Holekamp et al. 2007). Some engage in communal rearing, which may require complex "contracts" (Clutton-Brock and Parker 1995; Silk 2007). The nature and complexity of cooperation varies widely, and whereas passive cooperation appears to require little or no coordination (Brosnan et al. 2010), many predator species exhibit a high level of synchrony, coordination, and collaboration (Bailey et al. 2013) that does indicate the ability of one animal to attend to the behavior and state of partner animals (Tomasello et al. 1998; Emery et al. 2007; Drea and Carter 2009). All of these tasks are underpinned by effective communication, and communication efficiency has also been suggested as a driver of cognitive abilities (Dunbar 1993).

Cooperative hunting also introduces challenges not present in other collaborative activities, most notably attention to the dynamic behavior of other individuals, whether hunter or prey. In fact, it appears to be attention to conspecifics that characterizes the most sophisticated cooperation. In examining the behavior of cooperative hunters in the order Carnivora, Bailey et al. (2013) point out that the highest level of cooperation is characterized by behavior that is more influenced by the position and behavior of conspecifics, rather than the position and behavior of the prey item. This in itself would suggest a beneficial role for intraspecific communication. Hunting also requires a (temporary) suppression of within-group aggression, and exercising restraint under highly aroused conditions; both of which are features of social groups with sophisticated communicative systems (Bailey et al. 2013). Although few examples exist of vocal communication actually directing the course of a cooperative hunt, there are some indications that killer whales *Orcinus orca* use their vocal abilities coordinate seal hunting by "wave-washing" (Pitman and Durban 2012).

The connection between cooperation and cognition however remains largely opaque to us. Despite intuitive ideas that sophisticated cooperative tasks, such as wolf pack hunting, must imply human-like abilities of foresight, planning, and even sense of self/other, many mathematical simulations have shown remarkably sophisticated patterns of cooperative or goal-directed behavior can be explained by simple rules (Muro et al. 2011; Strombom et al. 2014). Furthermore, detailed examination of multiple taxa has not provided convincing evidence that cooperation is underpinned by sophisticated cognitive abilities (Smith et al. 2012). It therefore remains an open question whether human mental abilities such as Theory of Mind arose from positive selection for problem solving such as cooperative hunting, or whether cognitive abilities arose first to contend with complex social relationships, and later were put to use to solve ecological problems (Barrett et al. 2007; Seed et al. 2008). However, even if as has been proposed (Gavrilets 2015), complex cognition arose from inter-group conflict, rather than intra-group cooperation, many social carnivore species show a range of inter- as well as intra-group behaviors similar to those exhibited by humans—such as that seen in the cooperative territorial defence in wolves (Harrington and Mech 1983).

We have special relationships with several carnivores forged by a history of domestication. While we know that domestication selects for a series of behavioral and morphological traits, we have yet to understand how it has selected for specific cognitive abilities and how it may have simplified communication. However, some research suggests that domestication of dogs has preserved a communicative system that may at least in part support inter-specific collaborative hunting (Hare and Tomasello 2005).

Others (Smith et al. 2012) have noted how and why social carnivores are an important out-group for studies of cooperation in mammals and humans, principally because cooperation and sociality has independently evolved in carnivores. Thus, a number of questions about the mechanisms underpinning these independent evolutions permit us to search for general rules.

If the goal is to understand differences in species and to study the evolution of mechanistic diversity, we suggest that a concrete model linking CCC is required (Figure 1). A tripartite behavioral complex such as CCC necessarily involves multiple interactions between the

three elements of behavior (cooperation, cognition, and communication), and also the external environment, both physical and social. An integrative framework similar to that shown in Figure 1 can aid in formalizing and specifying these relationships, with a view to developing experimental and observational assessments of the relative role of each in the evolution of the complex as a whole.

Our model recognizes that the acoustic structure of vocalizations is influenced by both the physical environment, which both creates a context and may also influence the emotional valence of a signal and the social environment. We know that more socially complex species produce more complex repertoires and that social stress might modify the acoustic structure of vocalizations in ways that would be predicted by then nonlinearity and fear hypothesis (Blumstein and Récapet 2009; Blumstein et al. 2010). The physical and social environment also places constraints on the communicative and cognitive abilities of species, as well as driving them to particular solutions to fitness challenges, that together define the animal's niche (Holekamp et al. 2013; Barrett and Würsig 2014).

We also suggest that the relationships between CCC should continue to embrace their Tinbergen diversity. For instance, there are classical studies of the development of both sociality and communication. New techniques, such as the animal model (Kruuk 2004), permit us to study development in a variance decomposition way that reveals different factors may explain variation in signal structure at different age classes. For instance, the maternal environment explains significant variation in the structure of juvenile yellow-bellied marmot alarm calls, while variation in the structure of older animals is heritable (Blumstein 2013). Adopting a trait-decomposition approach to study the evolution of complex abilities—both social and cognitive—might be possible for properly defined traits. Further, the sociogenomic revolution creates the opportunity to dive even deeper to identify both homology and homeoplasy in communicative, social, and cognitive traits (Robinson et al. 2005).

Field studies of carnivores are often, by their very nature, long term. We believe this provides yet another call for the value of long-term research because the data required to understand the CCC nexus require long-term data and thus long-term financial support. In an age of budget cuts for scientific research, funding for long-term field studies is extremely difficult to obtain. Carnivore research is not inexpensive and thus articulating the need and value of a deeper understanding of the nexus is essential.

This special issue emerged from a symposium at a scientific meeting—Behaviour 2015 in Cairns, Australia—where five speakers shared insights into the relationship between CCC from studies of meerkats *Suricata suricatta*, feral cats *Felis silvestris catus*, spotted hyenas *Crocuta crocuta*, dogs *Canis familiaris* and wolves *Canis lupus*, and lions *Panthera leo*. We are pleased to have solicited additional articles from other contributors for this special issue.

Dunston et al. (2016) address the crucial question of the interplay between sociality (as measured by social network analysis), and varying conditions of the physical environment. African lions are highly social and highly cooperative hunters that are subject to intense conservation challenges. By comparing the social structure of both wild and captive-bred prides, Dunston et al. not only provide answers to important conservation questions of how and whether to reintroduce captive-bred animals into the wild, but also open a window into the fundamental nature of the social network in cooperative species. Captive-bred lions show very similar social structure to wild prides, indicating that specific aspects of how they interact with others are highly canalized are innate and likely adapted to their particular niche.

Staying in Africa, Lehmann et al. (2016) examine the highly sophisticated cooperative defence mechanisms of spotted hyenas. These social breeders use complex vocal communication to mediate their defensive responses to challenges from other species, particularly lions. Hyena mobbing calls represent one of the most sophisticated examples of vocal-mediated cooperative behavior, and Lehmann et al. show how the recruitment of additional hyenas greatly impacts the likely outcome of a potential conflict with lions. This study system represents one of the most promising avenues for investigating the interplay between sociality and communication, and Lehmann et al. lay the basis for future research in this direction.

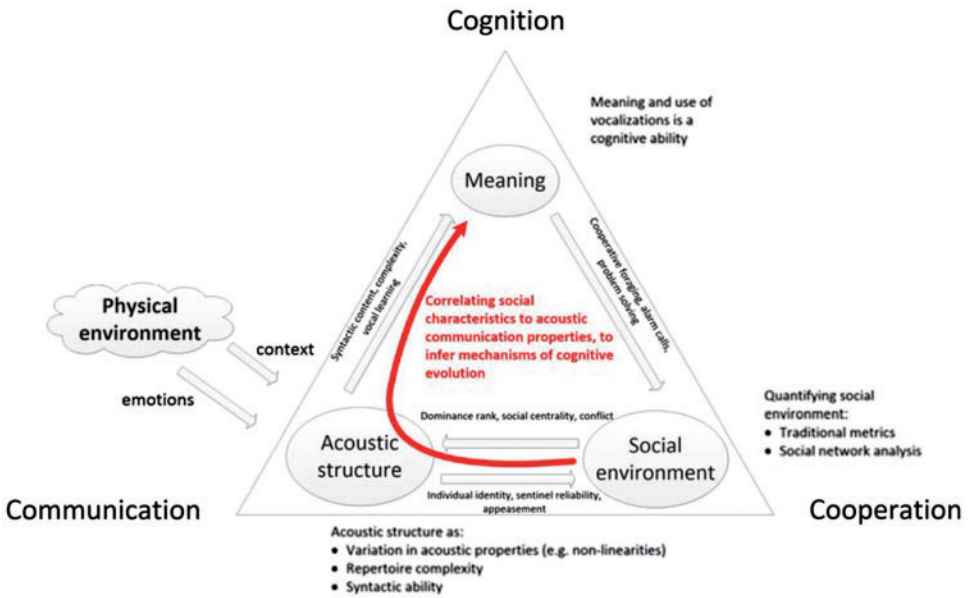

Figure 1. An integrative model linking cooperation, acoustic communication, and cognition that recognizes the important role that the physical environment plays in structuring signals, as well as the factors that influence the evolution of meaning and how increased cognitive abilities can facilitate the evolution of more complex cooperation.

Complex social cooperation is also found in wolves *C. lupus* and their close relatives, domestic dogs *C. familiaris*. Dale et al. (2017) examine one of the more perplexing aspects of social cooperation: food sharing between unrelated individuals. Despite the close relationship between these two species, the physical and social environments are very different, with wolves living in small, stable, mostly kin-groups, whereas free-ranging dogs live in large, multi-male/multi-female, mostly non-kin aggregations. The findings of Dale et al. that reciprocal provisioning non-kin is more common in more complex, less kin-related groups, provide an interesting hypothesis for the potential evolutionary pathways to the formation of more complex social groups.

Feral cats, as well as feral dogs, provide a surprising addition to our knowledge of the interplay between social cooperation and vocal communication. Once considered to be essentially solitary animals, Owens et al. (2017) show that feral cats have an unexpectedly complex vocal repertoire, which seems consistent with our current understanding of the social structure of feral cat colonies that often consist of large numbers of animals, displaying cooperative behavior such as alloparental care. However, studies of complex communicative behavior in feral cats have been frustrated by a lack of a consistent methodology for describing these vocalizations. Owens et al. bring the study of cat vocal behavior into line with the work done on other species, by providing an acoustic hierarchical classification system, which allows investigation of the nature and role of vocal signals in this well-known but under-studied animal.

One important question when examining the interplay between environment and behavior is the role of phylogeny and genetic drift. The many subspecies of gray wolf have become genetically isolated relatively recently, and provide an interesting study system for investigating the adaptive role of vocal communication in cooperative species. Hennelly et al. (2017) compare the vocal behavior of three smaller-bodied, more basal wolf lineages, to that of the larger Holoarctic subspecies. Howling is a long-range communication modality, vital to maintaining the cooperative social structure of wolf packs, and one could speculate that adaptive forces may shape the acoustic nature of howling to suit the different niches of each subspecies. However, Hennelly et al. show that the Himalayan wolf *C. l. chanco* uses vocalizations that are acoustically distinct from those of similarly sized North African wolves *C. l. lupaster* and Indian wolves *C. l. pallipes*. Phylogenetic constraints as well as habitat differences may underlie different vocal behaviors, adding yet another dimension to the raft of factors both driving and constraining the evolution of complex social, cognitive, and communicative behavior.

Finally, Wyman et al. (2017) examine the role of social effects in modifying the communicative behavior of cooperative group-living meerkats. Information reliability, and the role of dominance and signaler identity (shown on the lower axis of Figure 1) play a major role in shaping the acoustic structure of a group's communication signals. Meerkats cooperatively provision pups while foraging, but the loud and persistent begging calls of the young cause a marked alteration in adult cohesion calling. Individuals must trade off the various constraints driving a particular communicative behavior, in the light of changing social group composition (e.g., the presence of pups). Such changes in acoustic structure with changing social context may provide a pathway to more context-specific communication, and thence to communicative meaning, and the cognitive skills necessary to interpret that meaning.

We are thrilled by the opportunities that knowledge of cognitive abilities has for both welfare and conservation. All the studies in this issue raise questions that are relevant for understanding the nature and evolution of complex cognition and cooperation, but also address real-world questions of conservation and management. By understanding better the nature of the social behavior of some of the world's most charismatic animals, we can make better decisions to mitigate conflict with humans, and preserve their presence in the wild.

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